

# Additional material of the enigmatic Early Miocene mammal *Kelba* and its relationship to the order Ptolemaiida

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*Kelba quadeemae*, a fossil mammal from the Early Miocene of East Africa, was originally named on the basis of three isolated upper molars. *Kelba* has previously been interpreted as a creodont, a pantolestid, an insectivoran, and a hemigaline viverrid. The true affinities of this taxon have remained unclear because of the limited material and its unique morphology relative to other Miocene African mammals. New material of *Kelba* from several East African Miocene localities, most notably a skull from the Early Miocene locality of Songhor in Western Kenya, permits analysis of the affinities of *Kelba* and documents the lower dentition of this taxon. Morphological comparison of this new material clearly demonstrates that *Kelba* is a member of the order Ptolemaiida, a poorly understood group whose fossil record was previously restricted to the Oligocene Fayum deposits of northern Egypt. Phylogenetic analysis supports the monophyly of the Ptolemaiida, including *Kelba*, and recovers two monophyletic clades within the order. We provide new family names for these groups and an emended diagnosis for the order. The discovery of ptolemaiids from the Miocene of East Africa is significant because it extends the known temporal range of the order by >10 million years and the geographic range by >3,200 km. Although the higher-level affinities of the Ptolemaiida remain obscure, their unique morphology and distribution through a larger area of Africa (and exclusively Africa) lend support to the idea that Ptolemaiida may have an ancient African origin.

Afrotheria | Fayum | Kenya | Paleogene | Placentalia

*Kelba quadeemae* was described on the basis of three isolated upper molars from the Lower Miocene of eastern Africa (1). When he originally described the genus, Savage (1) placed *Kelba* in the subfamily Oxycloeninae (suborder Creodonta), then considered part of the order Carnivora but now viewed as a subfamily of the enigmatic “condylarthran” family Arctocyonidae (2). Oxycloenines are otherwise known from the Paleocene and Lower Eocene of North America (2), and *K. quadeemae* would constitute its only record outside that continent. This was a less than satisfactory attribution, but because of the primitive tribosphenic pattern of *Kelba*'s upper molars, it has proven difficult to determine the placement of *Kelba* within placental mammals.

Van Valen (3) noted similarities shared by *K. quadeemae* and early Paleogene *Pantolestes* (suborder Pantolesta, order Cimolestida) and suggested that *K. quadeemae* might represent the upper dentition (not known at the time) of Ptolemaiidae, which he included in the Pantolestidae, following Schlosser (4). Butler (5) placed *K. quadeemae* in the Ptolemaiidae (then considered members of Insectivora) based on Van Valen's suggestion (3). Savage and Russell (6) placed *Kelba* in “?Pantolesta,” whereas McKenna and Bell (7), in their overview of mammalian classification, place *K. quadeemae* in the Carnivora without providing a subordinal allocation. Most recently, Morales *et al.* (8) have suggested that *Kelba* belongs in the subfamily Hemigalinae of the

Viverridae (Carnivora) and is synonymous with two other poorly known mammals from Songhor, *Kenyalutra songhorensis* (9) and *Ndamathaia kubwa* (10).

All of these suggestions are problematic because they each require significant temporal and geographic range extensions. Given the original hypothesis of a few isolated molars of generalized tribosphenic pattern, it has not been possible to state with certainty to which of these groups (if any) *Kelba* is most closely related. It has always been clear, however, that *Kelba* represents a unique taxon in the East African Miocene record and that its affinities were most likely to be found among Paleogene mammals of the Old World.

In recent years, material of *Kelba* has been discovered at several sites in East Africa and stored in the Kenya National Museums in Nairobi (KNM). This material makes it clear that *Kelba* is indeed a ptolemaid, as originally suggested by Van Valen (3) and Butler (5). In this article, we describe this material, including a partial cranium with complete dentition (KNM SO 23296), and material that we believe represents the lower dentition of *Kelba*, which was previously unknown.

## Background on Ptolemaiids

Ptolemaiida is a poorly known order whose relationships with other placental mammals remain unresolved. The ptolemaidian dentition combines a primitive tribosphenic molar pattern with a set of unique dental specializations not seen in other mammals. Until now, Ptolemaiida were known exclusively from Oligocene deposits in the Jebel Qatrani Formation of the Fayum Depression in northern Egypt (11–14).

Osborn (11) named the family “Ptolemaiidae” on the basis of a single jaw of *Ptolemaia lyonsi* from the Fayum, stating that the group was of “uncertain ordinal status” and suggesting that it might represent a new order of mammals. Since then, the Ptolemaiidae have been considered as a group within the pantolestids (3, 6, 12) or “insectivores” (5), although Simons and Gingerich (13) left it as order *incertae sedis*. More recently, Simons and Bown (14) elevated the group to its own order, the Ptolemaiida. There are currently three recognized genera, *Ptolemaia*, *Qarunavus*, and *Cleopatrodon*, with five species (11–15), all known exclusively from the Fayum of Egypt. *P. lyonsi* and *Ptolemaia grangeri* are documented from Quarries A (≈34–33 Ma) and V (≈32–31 Ma), respectively (14–16); *Qarunavus*

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Abbreviations: KNM, Kenya National Museums, Nairobi; NHM, Natural History Museum, Department of Paleontology, London; I, upper incisor; C, upper canine; P, upper premolar; M, upper molar; p, lower premolar; m, lower molar.

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**Table 1. List of material attributed to *Kelba quadeemae***

| Specimen no.               | Part            | Locality            | Age, Ma | Refs.  |
|----------------------------|-----------------|---------------------|---------|--------|
| KNM ME 14                  | Mandible        | Meswa Bridge, Kenya | 22      | 19, 20 |
| KNM SO 23296               | Partial cranium | Songhor, Kenya      | 19.5    | 19, 20 |
| KNM SO 1690                | p2              | Songhor, Kenya      | 19.5    | 19, 20 |
| KNM SO 5669                | M2              | Songhor, Kenya      | 19.5    | 19, 20 |
| KNM SO 1555                | M2              | Songhor, Kenya      | 19.5    | 19, 20 |
| KNM LG 470                 | m2              | Legetet, Kenya      | 19.5    | 19, 20 |
| KNM CA 2821                | m1              | Chamtwaru, Kenya    | 19.5    | 19, 20 |
| M 19095 (1)                | M3              | Napak, Uganda       | 19.5    | 19     |
| M 19087- Holotype (1)      | M1?             | Rusinga, Kenya      | 18.3    | 18     |
| KNM MW 181 (1-as CMF 4028) | M1?             | Mfwanganu, Kenya    | 18.3    | 18     |
| KNM BN 10036               | m2              | BPRP Site 38, Kenya | 12.5    | 21     |

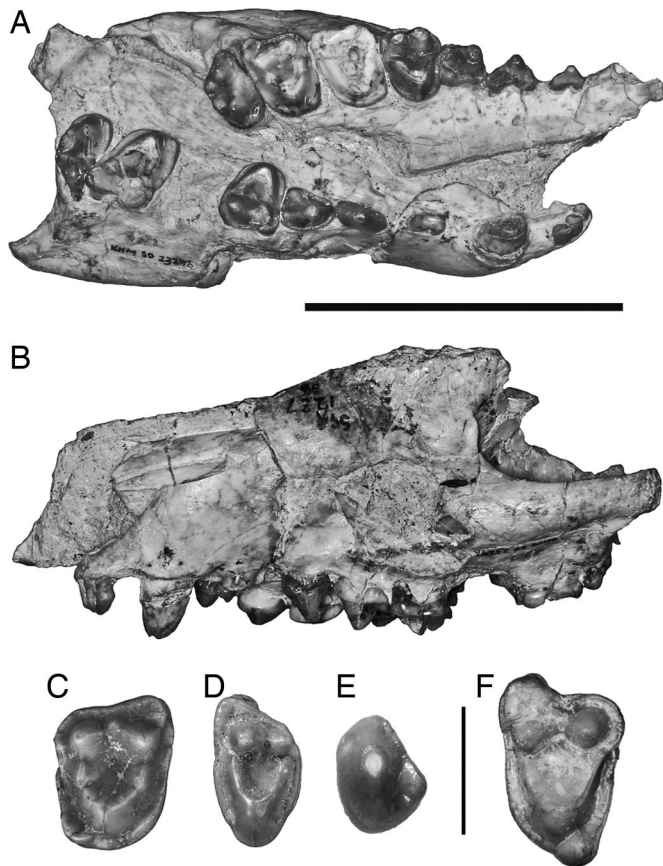
*meyeri* is known from a single juvenile mandible from Fayum Quarry A (13, 16); and *Cleopatorodon ayeshae* and *Cleopatorodon robusta* are known from Quarries V and I (30.2–29.4 Ma) (12, 16). In addition, there is a new and undescribed ptolemaiid from the older Fayum Locality BQ-2 in the Birket Qarun Formation. This site has been dated to ≈37 Ma (16, 17).

*Kelba* is now known from several Miocene localities in East Africa (Table 1). The type specimen is from Rusinga Island in Lake Victoria, which is dated to 18.3 Ma, as are deposits on the nearby Mfwanganu Island (18), but the majority of the new

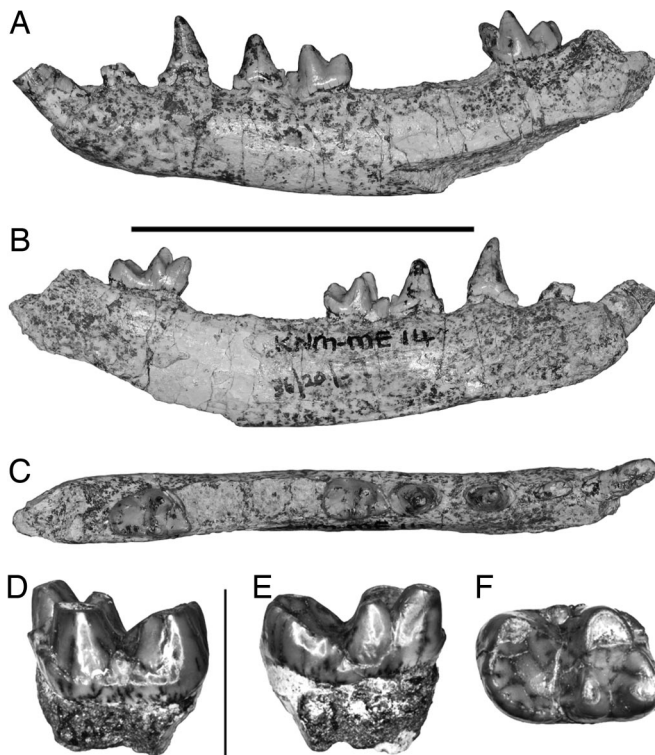
material comes from sites that are ≈1 Ma older. The most significant new specimen is a partial cranium with complete upper dentition (Fig. 1 A and B) that comes from Songhor in western Kenya, radiometrically dated to 19.5 Ma (19, 20). Additional material comes from the nearby localities of Legetet, Chamtwara (Kenya), and Napak (Uganda), which are roughly contemporaneous with Songhor (20). A mandible (Fig. 2 A–C) from the western Kenyan site of Meswa Bridge is slightly older, likely between 23 and 21 Ma (19, 20). The youngest specimen is a lower molar (Fig. 2 D–F) from the Kabarsero area in the Ngorora Formation of the Tugen Hills, Central Kenya. This site (Baringo Paleontological Research Project site #38) is only 12.5 Ma (21) and is by far the most recent occurrence of a ptolemaiid.

**Results**

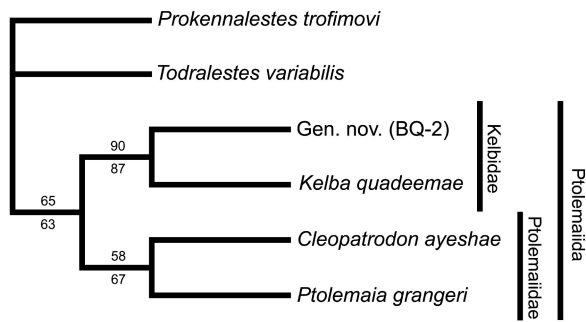
Phylogenetic analysis (Fig. 3) supports the monophyly of a ptolemaiidan clade that includes *Kelba*. We also find two mono-



**Fig. 1. Upper dentition of *Kelba*.** (A) Occlusal view of the KNM SO 23296 partial cranium, showing right P1–P4 and M1–M3; left I1–I3, C, P1–P4, and M2–M3. (B) Left lateral view of same. (Scale bar for A and B: 50 mm.) (C) Occlusal view of holotype M1? (NHM M 19087). (D) Occlusal view of M3 (NHM M 19095). (E) Right P3 of *Cleopatorodon* (Duke Lemur Center, Division of Fossil Primates, 9468), reported as left P3 in Simons and Bown (11). (F) Occlusal view of KNM SO 5669, M2 (Scale bar for C–F: 10 mm.)



**Fig. 2. Lower dentition of *Kelba*.** (A–C) Buccal (A), lingual (B), and occlusal (C) views of mandible KNM ME 14. (Scale bar for A–C: 50 mm.) (D–F) Buccal (D), lingual (E), and occlusal (F) views of KNM BN 10036, m2 attributed to *Kelba* sp. (Scale bar for D–F: 10 mm.)



**Fig. 3.** Strict consensus tree for the Ptolemaiida. Only one tree was recovered in ordered/unordered analysis (ordered tree length = 32; consistency index = 0.656; unordered tree length = 31; consistency index = 0.677). Numbers along the branches represent bootstrap support (1,000 repetitions) with multistate characters ordered (above branch) and unordered (below branch).

phyletic clades within the order Ptolemaiida: one including the previously described ptolemaiids *Cleopatrodon* and *Ptolemaia* and the other including *Kelba* and the oldest known ptolemaiidan, an undescribed new genus from Locality BQ-2.

Below, we emend the diagnosis of the order Ptolemaiida and family Ptolemaiidae, and erect a new family within Ptolemaiida.

### Systematic Paleontology

#### Ptolemaiida, Simons and Bown, 1995.

**Type genus.** *Ptolemaia*, Osborn, 1908.

**Included taxa.** The type genus; *Cleopatrodon*, Bown and Simons, 1987; *Qarunavus*, Simons and Gingerich, 1974; *Kelba*, Savage, 1965; undescribed new genus from Quarry BQ-2, Fayum.

**Emended diagnosis.** The order Ptolemaiida is difficult to diagnose because the higher-level affinities of the order are unknown, making outgroup selection problematic. Ptolemaiidans can be distinguished relative to all mammals by the combination of the following features: three upper incisors arranged in a parabolic arch, with upper incisor (I)3 well separated from the canine by a diastema; a single rooted canine; upper canines straight with striated enamel; upper premolar (P)3 with protocone shifted far posteriorly, with an accessory cusp distal to the paracone (seen in *Kelba* and *Cleopatrodon*; P3 not known in other taxa); upper molars with large protocone and well developed buccal cingulum; no preparacrista on upper molar (M)1 or M2; lower premolar (p)4 with large metaconid (reversed in *Cleopatrodon*); a long infraorbital canal with the anterior opening above P3; and a retracted nasal aperture (seen in lateral view) with premaxilla extending far ventrally relative to dorsal margin.

**Ptolemaiida, incertae sedis.** *Qarunavus meyeri*, Simons and Gingerich, 1974. Known only from a single juvenile mandible, it is not possible to place *Qarunavus* in either family at the present time.

#### Ptolemaiidae, Osborn, 1908.

**Type genus.** *Ptolemaia*, Osborn, 1908.

**Included taxa.** *Ptolemaia lyonsi*, Osborn, 1908; *Ptolemaia grangeri*, Bown and Simons, 1987; *Cleopatrodon ayeshae*, Bown and Simons, 1987; *Cleopatrodon robusta*, Bown and Simons, 1987.

**Emended diagnosis.** Metaconule present on P4; upper molars mesiodistally short and without mesial and distal cingula; bases of paracone and metacone fused on upper molars; postprotocrista of M1 and M2 do not meet with the metacone; no cristid obliqua on p4, but large hypoconid is present; mesiodistally short talonid basins on lower molars (m)1–m3; m3 paraconid closely situated to metaconid.

#### Kelbidae, nov. family.

**Type genus.** *Kelba*, Savage, 1965.

**Included taxa.** *Kelba quadeemae*, Savage, 1965; new undescribed genus from Locality BQ-2 in the Fayum, Egypt.

**Diagnosis.** Upper molars with mesial and distal cingula, paracone and metacone widely separated, premetacrista oriented buccally rather than mesially, and postprotocrista meeting with the lingual face of the metacone; mesostyle present on M1/2; p4 with trenchant cristid obliqua and large talonid basin; lower molar entocristids with cusps (also present in *Qarunavus*).

#### *Kelba quadeemae*, Savage, 1965.

**Holotype.** Natural History Museum, Department of Palaeontology, London (NHM) M19087, a left M1? described by Savage (1) as a right M2.

**Hypodigm.** See Table 1.

**Type locality.** Early Miocene, Rusinga Island, Lake Victoria, Kenya; radiometrically dated to 18.3 Ma (18).

**Emended diagnosis.** Metacone present on P4; upper molars with mesostyle positioned between metacone and paracone, metaconule and paraconule variably present on pre- and postprotocristae, mesial and distal cingula particularly well developed with shelf-like cusp (pericone) developed on mesiolingual cingulum; large metaconid on p4; lower molar entoconids small or absent, paraconid widely separated from other trigonid cusps.

**Description of *Kelba quadeemae*.** The most significant new specimen of *Kelba* is a crushed and distorted, but relatively complete, anterior part of a skull (KNM SO 23696; Fig. 1 A and B). The entire upper dentition is preserved. The lower dentition of *Kelba* is recognized for the first time, best represented by KNM ME 14, a left horizontal ramus with P1–P4 and M3 preserved (Fig. 2 A–C). The following description is based largely on these two specimens, with additional information for the upper and lower dentition from isolated teeth (Table 1; Figs. 1 and 2). Dental measurements and additional details of the morphology of *Kelba* can be found in the [supporting information \(SI\)](#).

**Cranial morphology.** The nasals have an anterior border with a strong central notch, whereas the medial and lateral ends are longer, giving it the shape of an inverted V. As in *Ptolemaia* (14), the lateral border of the nasal aperture inclines posteriorly, but in *Kelba*, the contact between the nasals and premaxilla occurs slightly further back, just above the midline of the canine. The sutures of the jugal and lacrimal are not visible and may be fused. The infraorbital foramen is situated far forward, approximately level with the anterior root of P3. The maxilla bulges out posterolaterally from this point until it forms the anterior root of the zygomatic arch; this region is far less robust in *Ptolemaia*. The space between this bulging part of the maxilla and the maxilla–nasal suture is gently dorsolaterally concave. The anterior orbital margin is ellipsoid and has a small, centrally located protrusion that may be the lacrimal tubercle. Both the sphenopalatine and dorsopalatine foramina are visible in the left orbit and are set in a common fossa. Ventrally, the incisive foramina are long and slender, as in *Ptolemaia*, and run from the distal margin of I3 to end posteriorly at the level of the middle of the canine. The posterior end of the palatine (visible on the left side) extends beyond M3 and appears to have a postpalatine torus. In *Ptolemaia*, the posterior palatine torus is much more gracile, and is situated medial to M3 rather than far posterior to that tooth as in *Kelba*.

**Upper dentition.** The upper incisors are arranged in a gentle arc. They are small relative to the size of the postcanine dentition. They have a cylindrical outline and are similar in morphology, with size increasing gradually from I1 to I3. The I3 is separated from the canine by a diastema. The upper canine is elliptical in cross-section, with a sharp posterior apex. It is

straight with finely striated enamel, and is separated from the P1 by a diastema.

P1 and P2 are slender teeth with the main cusps situated somewhat anterior to the midline of the tooth. A faint cingulum surrounds both teeth, but is more strongly developed in P2. The P3 has a distinct posterior accessory cusp, and a strong cingulum surrounds the tooth. There is a protocone at the posterolingual corner of the cingulum that causes the tooth to broaden out significantly. This tooth is quite similar to the P3 of *Cleopatorodon* (Fig. 1E).

The P4 is molariform. The metacone and paracone are bounded by a strong cingulum that runs along the entire buccal length of the tooth and around the antero- and posterobuccal corners. The protocone is large and V-shaped and has strong pre- and postprotocristae with no paraconule or metaconule. The preprotocrista and postprotocrista meet with the mesial and distal cingula, respectively, rather than with the lingual face of the paracone and metacone. The protocone is bordered mesio- and distolingually by strong cingula that are not fully continuous.

The first and second upper molars are the most common elements in the *Kelba* collection, and they show a great deal of morphological variation. In general, the teeth are broad and square with strong buccal, mesial, and distal cingula. They have three roots. The paracone and metacone are subequal in size, whereas the protocone is much larger. There is a small mesostyle positioned buccally between the paracone and metacone. The protocone is V-shaped, with strong pre- and postprotocristae. In unworn specimens, a paraconule and metaconule may be present, although they can be very weakly developed. There is a small postmetacrista that sometimes terminates in a small metastyle. The buccal cingulum is very wide and creates a buccal shelf. The margin of the buccal cingulum is crenulated in unworn specimens. There is a small cusp on the cingulum at the anterolingual corner of the tooth, which we refer to as the pericone.

The right M1 is very worn on KNM SO 23296, whereas the left is absent. However, M1 may be represented by the holotype (Fig. 1C) originally described as “M2” by Savage (1). Overall, M1 is similar to the better represented M2, but is smaller and has a less prominent metastyle, giving it a more square occlusal outline. In the holotype (M 19087), the preprotocrista and postprotocrista meet with the lingual faces of the paracone and metacone, respectively, rather than with the mesial and distal cingula, and strong para- and metaconules are present.

The M2 is the largest cheek tooth. The cingulum is discontinuous on the lingual aspect of the protocone. The buccal shelf is larger posteriorly than in M1, often with a larger metastyle. The postprotocrista meets with the lingual face of the metacone, but the preprotocrista appears to meet with the mesial cingulum, as in P4. There does not appear to be either a paraconule or metaconule.

The M3 (Fig. 1D) is similar in morphology to M1 and M2 but is anteroposteriorly foreshortened and has only two roots. The paracone is much larger than the metacone and has a well developed cingulum on its buccal side. The postprotocrista meets with the metacone, whereas the preprotocrista meets with the mesial cingulum. This is the same condition seen in M2. A metaconule is always present, but the paraconule and pericone are variably present (both are present on KNM SO 23296 and absent in NHM M 19095). The cingula are stronger in KNM SO 23296 than in NHM M 19095, where there is no lingual cingulum at all.

The holotype is the only M1/2 that shows a well developed paraconule and metaconule. A metaconule (but not a paraconule) is preserved on all known M3s. The holotype is also the only upper molar in which the preprotocrista connects with the paracone, rather than with the mesial cingulum. These differences are intriguing, and it is for these reasons (along with size and the reduced metastyle) that we propose that the holotype

represents M1. However, it is also possible that there is a species difference between the holotype from Rusinga and the slightly older material from Songhor, Napak, Legetet, and Chamtwara (see Table 1). At present, we prefer to interpret these specimens as a single taxon, with the holotype as M1, because it is similar in size and occlusal morphology to the very worn M1 on the KNM SO 23296 skull.

KNM-SO 5669 (Fig. 1F) is an isolated upper right molar, most likely M2, that shows some interesting differences from the other M2s. It is mesiodistally shorter, with less developed mesial and distal cingula. The pericone is much larger than in other specimens, and although there is a broad cingulum posterobuccally, there is no metastyle (a variable feature). Like other M2s, there is a mesostyle (although it is very weak), and there is no trace of a paraconule or metaconule. Like the holotype, these morphological differences could indicate that multiple taxa are present in the *Kelba* hypodigm. Given that the only major differences are the mesiodistal length and the size of the pericone, and that there is a considerable degree of variation in the upper molar morphology in general, we choose to retain this specimen in *K. quadeemae* at present.

**Mandibular morphology.** The ramus is long and slender (Fig. 2 A–C). There are three mental foramina located under the premolars. The symphyseal rugosity is nearly horizontal and extends along the ventral part of the ramus to the back of p2.

**Lower dentition.** The lower canine is relatively procumbent and somewhat mediolaterally compressed. The p1 is two-rooted, small, and slender with the apex set well anterior to the middle of the tooth. The p2 is elliptical in cross-section and high-crowned. In KNM ME 14, the p2 appears to be implanted backwards in the jaw, which we believe is the true morphology and not a case of improper gluing. This may be a case of “extreme tooth rotation,” which is sometimes found in mammals (see ref. 22 and the SI). The p3 is symmetrical, with nearly vertical anterior and posterior faces. There is a cingulum surrounding the tooth and a well developed posterior accessory cusp.

The p4 is molariform. The protoconid is the tallest of the trigonid cusps and also the largest seen in the occlusal view. The metaconid is somewhat lower than the protoconid and set almost directly lingual to it. The talonid is low and broad, with a relatively tall hypoconid. There is a very low cusp and postcristid at the posterolingual corner, but no distinct entoconid. There is a weak cingulum along the buccal side of the tooth.

The alveoli in KNM ME 14 indicate that the size of the molariform cheek teeth increases gradually from p4 to m3. The lower molars have a generalized tribosphenic pattern with the trigonid cusps separated by deep notches and the metaconid directly lingual to the protoconid. The protoconid is the largest cusp, followed by the paraconid and metaconid. The talonid is only slightly buccolingually narrower than the trigonid, but there is a relatively deep hypoflexid. The anterobuccal margin of the tooth has a moderately strong cingulum, which wraps around the protoconid and continues to the distal end of the tooth in some specimens.

In m1 and m2, the talonid is longer than the trigonid. There is a small shelf present at the hypoflexid and, in general, the cingulids seem to be more developed than in m3. The m1 protoconid is relatively smaller. The hypoconid of m1 and m2 is well formed, but there is no trace of an entoconid.

In m3, the talonid is more buccolingually compressed and is also mesiodistally shorter than the talonids of m1 and m2. The trigonid has a taller protoconid and is relatively mesiodistally longer than in m1 and m2, largely because of the anterior placement of the paraconid. There is a crestiform entoconid set on the lingual side of the tooth and a small hypoconulid is present.

## Discussion

Although the idea that *Kelba* may represent a ptolemaiidan is not entirely new [for instance, Bown and Simons (12) considered *Kelba* in their diagnosis of the genus *Cleopatrodon*], this is the first time that there has been material of sufficient quality to firmly place this genus within the order Ptolemaiida. *Kelba* is the first ptolemaiidan to be recognized outside of the Fayum area of Egypt and supports earlier suggestions (12) that a larger early Tertiary radiation of ptolemaiidans probably existed within Africa. *Kelba* provides evidence of this radiation and also demonstrates that ptolemaiidans have a more extensive temporal range than had been expected, extending well into the Miocene.

The phylogenetic analysis presented here supports the monophyly of the Ptolemaiida. It is interesting that *Kelba* is placed as the sister taxon to the oldest known ptolemaiidan, the undescribed new genus from the Eocene Quarry BQ-2 ( $\approx 37$  Ma), rather than with the Oligocene ptolemaiids from the Jebel Qatrani Formation. Oligocene ptolemaiids, particularly *Ptolemaia*, show unique dental specializations that may have restricted the range of ecological niches that they could exploit (14). In contrast, *Kelba*'s molarized premolars and generalized molars would have allowed it to process a variety of foods. It is possible that the more generalized dental morphology of kelbids relative to the more specialized ptolemaiids may have allowed the former greater ecological flexibility, and could help to explain why kelbids persisted well into the Miocene, whereas ptolemaiids evidently did not.

**Diversity of Ptolemaiidans Within East Africa.** At present, we include all East African ptolemaiidan material in *K. quadeemae*, while acknowledging that the wide variation seen in the morphology of upper molars (particularly the holotype M 19087 and KNM SO 5669) may indicate that more than one species is present. At present, the material is too limited to justify recognition of more than one taxon.

The BN 10036 specimen from the Tugen Hills is particularly intriguing in that it comes from a locality (Baringo Paleontological Research Project Site #38) that is radiometrically dated to 12.5 Ma (21). It is identical in all respects to the m2 KNM-LG 470, but is very slightly smaller. Although this tooth is  $\approx 7$  Ma younger than the other *K. quadeemae* material, its close similarity to the much older lower molars from Songhor, Chamtwara, and Legetet suggests that it belongs in *K. quadeemae*. The similarity is particularly striking in view of the considerable variation seen in the lower molars of Paleogene ptolemaiidans. For now, we retain KNM BN 10036 in *K. quadeemae*, although discovery of additional ptolemaiidans from the Middle and Late Miocene could necessitate a specific or even generic distinction.

**Paleobiology.** With such limited material, it is difficult to imagine what the life habits of ptolemaiidans might have been. *Kelba* would have been a medium-sized animal likely weighing  $\approx 15$  kg (the size of a modern coyote, but more heavily built). The strong wear seen on the upper molars, particularly M1, of the skull KNM SO 23296 suggests that the diet of *Kelba* must have consisted of a rather abrasive material. *Ptolemaia*, which shows a combination of extreme hypsodonty and heavy wear indicative of vertical crushing, has been interpreted as an insect feeder (14, 15), although the heavy wear would also indicate regular ingestion of abrasive foods. *Kelba*'s teeth are not as specialized as those of *Ptolemaia* and the generalized morphology of the molars and molarized premolars indicate that it could have been capable of eating a wide variety of dietary items.

**Higher-Level Affinities of Ptolemaiida.** The position of the Ptolemaiida within mammals has long been unclear (14, 15) and unfortunately, the addition of *Kelba* to the order does little to

resolve this. Most commonly, ptolemaiidans have been considered relatives of the suborder Pantolestia (7, 23), largely because of a lack of other likely candidates, although it is generally assumed that the dental similarities between these groups are symplesiomorphies (12).

A plausible alternative is that the Ptolemaiida might be members of the superorder Afrotheria, which includes the modern orders Proboscidea (elephants), Hyracoidea (hyraxes or dassies), Sirenia (sea cows), Macroscelidea (elephant-shrews), Tubulidentata (aardvarks), Tenrecidae (tenrecs and other shrews), and Chrysochloridae (golden moles). Afrotheria is generally thought to have had an ancient (Late Cretaceous) origin on the Afro-Arabian landmass, where members of the group apparently evolved in relative isolation until the latest Oligocene (24, 25). The Afrotheria was originally identified on the basis of molecular analyses, and support for the monophyly of the superorder has, to date, been provided in numerous molecular phylogenetic studies (e.g., see ref. 26). Before these studies, the superorder was not recognized on morphological grounds and, even in retrospect, it has proven difficult to find morphological, and especially hard-tissue, synapomorphies for the group (27, 28). This is because the modern afrotherian orders are highly morphologically divergent from each other, making shared derived characters hard to identify.

The only currently recognized extinct orders of afrotherians are the Embrithopoda and the Desmostylia, both of which have close ties to extant afrotherians. The Embrithopoda are large terrestrial mammals, closely linked to the Proboscidea (29). The Desmostylia is an aquatic lineage that was formerly included with the Sirenia, but has since been given ordinal status because of its divergent morphology, although it is still judged to be closely related to the sirenians and proboscideans (30). That no other such groups have been identified may be because of researchers' natural tendency to look outside of Africa when searching for the affinities of poorly known African groups, but this is beginning to change. For example, it has recently been suggested that the hyaenodontid creodonts may have an African origin (31).

Biogeography provides some support for placing the Ptolemaiida within the Afrotheria. Before the unambiguous identification herein of *Kelba* as a member of this order, the biogeography of ptolemaiidans could not be used to support any specific position regarding their affinities, as they were restricted to a few sites from a very limited geographic area. However, with the identification of the first ptolemaiidan outside the Fayum Depression in East Africa, the status of Ptolemaiida as African endemics with an early Cenozoic origin is strongly corroborated and much of the previous speculation on the affinities of ptolemaiidans, which has focused on links with Eurasian (and even North American) groups, is rendered far less likely. In an updated supraordinal classification, Ptolemaiida might belong with, or within, Afroinsectiphillia (the clade containing aardvarks, elephant-shrews, golden moles, and tenrecs).

Linking Ptolemaiida with Afrotheria solely on the basis of biogeography is obviously tenuous, but some lines of morphological evidence do support the idea that they might belong in the superorder. There are no definitive hard-tissue synapomorphies of Afrotheria (28), but Seiffert (32) noted that, under the hypothesis of afroinsectiphillian monophyly, there are at least four possible dental synapomorphies of Afrotheria, all of which occur in *Kelba*: (i) p4 talonid and trigonid of similar breadth, (ii) a prominent p4 hypoconid, (iii) presence of a P4 metacone, and (iv) absence of parastyles on M1–2. Not all of these characters are found in all ptolemaiidans, so they might represent autapomorphies of *Kelba* or synapomorphies of a clade within Ptolemaiida. Simons and Gingerich (13) suggested that ptolemaiidans might be related to the tubulidentates, based on "broad mandibular and dental similarities" between *Ptolemaia* and the

modern aardvark *Orycteropus*, although dental tubules are not present in any known ptolemaiidan. Dental similarities between *Ptolemaia* and aardvarks include hypsodont molars that wear down to a flat surface; a long and shallow mandible with an elongated symphyseal region; and trigonids and talonids that are separated by lateral constrictions (13). In addition, we note that the peculiar V-shaped morphology of the anterior end of the nasals described above for *Kelba* (Fig. 1B) is very rare among mammals and is similar to the morphology seen in extant aardvarks. These similarities between ptolemaiidans and aardvarks are intriguing, but a convincing test of such a relationship will require discovery of new and more complete material.

Whatever the affinities of Ptolemaiida might be, the discovery of a ptolemaiidan from the Miocene of East Africa is important because it greatly extends the temporal and geographic range of this enigmatic group. The recognition of *Kelba* as a ptolemaiidan, so far removed temporally and geographically from the Fayum Eocene and Oligocene taxa, suggests that a much greater diversity of ptolemaiidans waits to be discovered, and highlights the paucity of our knowledge of the African Paleogene and early Neogene fossil record.

### Materials and Methods

We carried out a phylogenetic analysis (using PAUP\* 4.0b10; ref. 33) to determine the placement of *Kelba* relative to other taxa

within the order Ptolemaiida. The character matrix includes 19 characters of the upper and lower dentition, coded for six taxa including two outgroup taxa. The outgroups used are *Todralestes variabilis*, a primitive Late Paleocene placental mammal from North Africa (34), and *Prokennalestes trofimovi*, an Early Cretaceous form from Mongolia that falls outside the crown placental mammal clade (35). Further details on the analysis, including the list of characters, are provided as SI.

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